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XXXV. On *CHONDROSTEUS*, an Extinct Genus of the *Sturionidæ*, found in the *Lias Formation at Lyme Regis*. By Sir PHILIP DE MALPAS GREY EGERTON, *Bart., M.P., F.R.S., F.G.S. &c.*

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Genus *CHONDROSTEUS*, AGASSIZ.

(Subkingdom VERTEBRATA, Class PISCES, Order GONIOLEPIDOTI, Family STURIONIDÆ.)

Head covered with bony plates. Body short, deep, adpressed, devoid of dermal plates. Scapula and coracoid united. Dorsal fin advanced. Tail heterocerque. Fin-rays formula: P. 50; V. 50; D. 75; A. 30; C. 75. Endoskeleton partly ossified, partly cartilaginous.

The recognition of a member of the Sturgeon family in the fossil state is due to Professor AGASSIZ, whose quick perception detected in some fragmentary specimens, found in the lias shales at Lyme Regis, structural peculiarities which convinced him that this family was not unrepresented in the secondary strata of Great Britain. The specimens first discovered were portions of the caudal fin, and it was from the examination of these that he established the genus *Chondrosteus*, and determined its affinities to the Sturgeons. This result is noticed at page 280 of the 2nd part of the 2nd volume of the 'Poissons Fossiles,' but no description is there given; nor has the subject been since alluded to by the Professor, the engagements undertaken in the United States having put a stop to the preparation of the supplementary continuation of his great work on which he was engaged previous to his departure. Most of the specimens subsequently discovered appertain also to the caudal region. The massive proportions of the caudal fin, the strength of the fin-rays, and the thickness and hardness of the fulcral scales on the upper lobe, account for the preservation of these parts in more perfect condition than others less qualified to resist the destructive agencies to which they have been exposed. Recent discoveries have disclosed a chain of evidence connecting these specimens with others, some of which were formerly assigned to the Sauroid and Cœlacanthoid families. The first link was afforded by a specimen which, in addition to the lower lobe of the caudal fin, contained the anal fin; subsequently a specimen came to light having the ventral fins superadded to the anal and caudal fins; and lastly, a fine example in hard lias, showing the posterior part of the cranium, both pectoral fins, both ventral fins, the dorsal fin and the anal fin (Plate LXVII.). The snout and the tail are deficient. The study of this specimen, and more especially of the scapulocoracoid arch and its appendages, led to the identification of many other specimens of the anterior parts which were not before supposed to have belonged to this genus. The facts brought to

light by these discoveries, and the more extended observations based thereupon, fully corroborate the conclusion arrived at by Professor AGASSIZ, that this genus, although differing generically from the Sturgeons of the present epoch, belonged, nevertheless, to the same family. These facts I now proceed to particularize in detail, commencing with a general description of the most perfect specimen, and proceeding step by step through the anatomical characters displayed in the several specimens I have examined, so far as their state of preservation will allow.

The most perfect specimen yet discovered (Plate LXVII.) is contained in a nodule of indurated lias. The rostral and caudal extremities are deficient, and it is otherwise much injured by the attempts to relieve it from the matrix in which it is imbedded. Excluding what remains of the head, and measuring from the articulation of the pectoral fin with the scapulocoracoid arch to the hinder margin of the anal fin, the length of the trunk is 15 inches. The greatest vertical depth is immediately in front of the dorsal fin, where it measures 6 inches. In a recent Sturgeon having the same longitudinal dimensions, the greatest vertical depth is only 3 inches, or in proportion to the length as 1 to 5, the relative proportions in the fossil being as 2 to 5. The comparative measurements are more disproportionate when applied to a restoration of the fossil genus. By selecting from the numerous specimens which have been found, a tail of a size corresponding with the other parts of the individual under description, and adjusting it thereto, the additional length obtained is 9 inches, making a total length of 24 inches from the attachment of the pectoral fin to the extremity of the upper lobe of the tail. The measurement of the corresponding part in the recent Sturgeon gives an increase of  $7\frac{1}{2}$  inches, or a total length of  $22\frac{1}{2}$  inches; the result being that the proportion of depth to length in the fossil is as 1 to 4, and in the recent fish as 1 to  $7\frac{1}{2}$ . The vertical diameter of the fossil at the point of fracture behind the anal fin is  $4\frac{1}{2}$  inches, the corresponding measurement of the recent fish is only 1 inch. It will be apparent from these dimensions that the Sturgeon of the lias differs from the existing Sturgeons in having a shorter and more bulky body, deepest in its middle portion, and contracting very gradually posteriorly as far as the anal fin. It is shown by other specimens that the diminution of bulk behind this point was more rapid down to the point whence the caudal fin expands. The breadth of the body was not, as it is in the Sturgeon of the present day, commensurate with the depth; for it is evident, from the proximity of the pectoral and ventral fins of either side to their fellows, that the sides of the fish were more flattened, and that the horizontal diameter of the body was considerably less than the vertical one. However striking and distinctive these proportions may be, compared with the graceful and taper outlines of the recent Sturgeons, other characters are afforded by the structure, form and position of the natatory organs, equally corroborative of generic difference.

The fins in all the recent Sturgeons are thus arranged:—the ventral fins are situated at the commencement of the posterior third segment of the body; the anal fin occupies a median position between these fins and the lobe of the tail, whilst the dorsal

fin is placed above the anal fin, having its anterior rays a little in advance of the first rays of that fin. In *Chondrosteus* the ventral fins are found midway between the pectoral fins and the tail; the dorsal fin is immediately above the ventral fins, and the anal fin approximated to the lower lobe of the tail. As regards size, all the fins are proportionately larger than those of the existing Sturgeons, as might naturally be inferred from the greater bulk of the fish. In proceeding to give a detailed description of the organs of locomotion and their associated parts, I commence with the bony framework which affords attachment and support to the pectoral fins; premising that the letters and numbers by which the several parts are designated on the drawings are those employed by Professor OWEN in his tabular notation of the homologies of the Vertebrate Skeleton.

*Scapular Arch and its Appendages.*—In the recent Sturgeons the strong bony girdle encircling the thoracic region of the trunk and providing a firm attachment for the large pectoral fins, is composed of three elements on either side, the suprascapular, the scapular, and the coracoid. In the extinct genus this number is reduced to two by the coalescence of the two latter to form a single bone (Plates LXVIII. fig. 1, and LXIX.<sup>51, 52</sup>). This scapulocoracoid bone, from its size and comparative hardness, is more frequently preserved and more perfectly displayed than any other of the constituent parts of the cranial framework. The external portion is crescentic, the concavity being anterior for the reception of the posterior margin of the opercular flap. At the point of attachment of the pectoral fin the bone is thick and rounded; the upper or scapular portion expands gradually into a triangular plate, thinning off towards the upper extremity for adjustment with the suprascapular bone; the lower or coracoid portion also expands as it descends, sweeping under the thorax and meeting the corresponding bone of the opposite side on the median line. The exposed surfaces of these bones are prettily ornamented with sharp undulating asperities, not unlike the surface ornament of the shell of *Pholas crispata*. Anteriorly each scapulocoracoid expands into a broad concave plate, directed inwards and forming the platform of the branchial cavity, and partitioning it off from the thoracic cavity. This portion of the bone has the surface perfectly smooth. The upper or suprascapular member of the arch (Plate LXIX.<sup>50</sup>) overlaps the extremity of the scapulocoracoid bone, and extends thence to the occipital region of the skull. It is of slender dimensions compared with the homologous bone of the recent Sturgeons. The ornamentation characteristic of the external portion of the scapulocoracoid bones is continued along the anterior margin of the suprascapular, but the greater portion of the bone seems to have been invested with the dermal integument; in this respect corresponding with the homologous bone in the ordinary ganoid fishes. The pectoral fins (Plates LXVII., LXVIII. fig. 1, and LXIX. P) are attached to the scapulocoracoids immediately behind the posterior angles of these bones. They are proportionately much broader and more rounded at their extremities than these organs of the recent Sturgeon, but the anterior ray is not nearly so strong. They have no representatives of radius, ulna, or carpus, but the fin-rays are articulated to a series of strong metacarpal bones, of which



those supporting the hinder rays are the longest (Plate LXIX. 57). Each metacarpal bone seems to have given attachment to several of the rays. The first ray is more massive than the succeeding ones, and is considerably shorter. It appears to be formed by the coalescence of two or more rays, and is subject to variations in this respect consequent, it may be, on the age of the individual. The surface is corrugated at the base and longitudinally sulcated above. The succeeding rays are about fifty in number. The anterior ones increase successively in length as they recede from the first or principal ray as far as the seventh or eighth ray, at which point the maximum extent of the fin is attained; and hence the fin-rays decrease gradually to the hinder margin of the fin. A few of the last rays lose their round character and become broad and inflexible triangular plates attached by their apices, and dilated posteriorly towards their distal extremities. The principal rays continue single for a considerable distance from the metacarpus, without either bifurcations or transverse joints; but in the more remote portions of the organ dichotomizations and joints are very numerous. In all the other fins the transverse articulations are continued to the base of the rays. The surface of the pectoral fin is irregularly beset with small asperities, a character which serves to distinguish a mere fragment of this fin from that of any other fossil fish with which I am acquainted. The dimensions of this fin, compared with the pectoral fin of the recent specimen already referred to in the other measurements, are as follows:—Recent Sturgeon 3 inches long by  $1\frac{1}{2}$  wide; Fossil,  $5\frac{1}{2}$  inches long by  $3\frac{1}{2}$  wide. The interval between the fins is 3 inches in the recent and 4 inches in the fossil fish, from the innermost rays of one fin to the corresponding rays of the other.

*Ventral Fins* (Plate LXVII. V).—No traces of pubic bones have as yet been found in the specimens I have examined, but in one where the base of the ventral fin is preserved, the constituent fin-rays are seen to be attached to a series of short styliiform ossicles. These tarso-metatarsal bones occur in the recent Sturgeon in a semicartilaginous condition, and in the Polypterus, but they are not found in the generality of recent osseous fishes. The ventral fin, when expanded, forms a nearly equilateral triangle, the sides of which measure about  $2\frac{3}{4}$  inches each. It is composed of more than fifty rays. These increase gradually in length from the first to the twelfth, which is the longest. They are gracefully curved, and are frequently subdivided both longitudinally and transversely. The interval between the fins is 2 inches; in the recent specimen it is 1 inch.

*Dorsal Fin* (Plate LXVII. D).—The dorsal fin is situated about the middle of the back, immediately above the ventral fins, extending over a space of  $4\frac{1}{2}$  inches, and measuring  $3\frac{1}{2}$  inches in height. It contains between seventy and eighty rays. Of these a few of the anterior rays are short and single, representing the fulcral scales common to many genera of ganoid fishes. They are succeeded by thick, jointed rays, increasing successively in height as far as the fourteenth, and thence decreasing gradually to the posterior termination of the fin. The rays bifurcate at some distance from their bases, and are frequently subdivided as they recede from the body. The transverse joints

commence near the insertions of the rays, and are repeated at shorter intervals on the posterior parts of the fin. The form of the dorsal fin, when expanded, represents a right-angled triangle, the rectangle occupying the apex, and the posterior angle being rather more acute than the anterior one, if the fulcral rays are not taken into account. Compared with the homologous organ of the Sturgeon, it is remarkable for its greater proportional expansion and strength. The comparison with the recent specimen employed in all the comparative measurements, gives the dimensions of 2 inches by  $1\frac{1}{2}$  inch for the Sturgeon, and  $4\frac{1}{2}$  inches by  $3\frac{1}{2}$  inches for the fossil. The former contains thirty-five rays, the latter probably eighty.

*Anal Fin* (Plates LXVII. and LXX. A).—The anal fin is placed nearer to the base of the caudal fin than to the ventral fins. It is the smallest of the natatory organs in the fossil genus, whereas the ventral fins are the smallest in the recent Sturgeon. The interhæmal spines supporting the fin are ten or twelve in number, elongated, slightly arched, and flattened at the articular extremities (Plate LXX. *i h*). The fin-rays are above thirty in number, and more slender than those of the dorsal fin. The lateral surfaces are subangular and not rounded, as in the dorsal and ventral fins. The transverse joints are frequent. The decrement in the length of the rays, from the anterior to the posterior limit of the fin, is very rapid, the posterior rays being short, slender, and finely fimbriate. The form of the fin is that of an isosceles triangle, broader at the base and less acute at the apex than the corresponding fin of the recent Sturgeon.

*Caudal Fin* (Plate LXX. C).—In all essential structural points the caudal fin of *Chondrosteus* corresponds closely with that of the recent Sturgeons. It differs, however, in form and relative proportions. It is considerably broader and more massive; the lobes are more divergent; the upper lobe is less acutely prolonged, and the lower one more nearly the length of the upper one. The point of divergence of the lobes is on a line with the axis of the body, so that the two halves are more symmetrical than in the tail of the Sturgeon. The upper border of the fin is composed of a single row of strong chevron-shaped fulcral scales, elongating in succession as they extend towards the extremity of the tail. These scales are imbricated, and each had a deep median sulcus at its base for the attachment of the preceding scale of the series. This portion of the caudal organ is further strengthened by a set of short spatulate neurapophyses (Plate LXX. C, *n a*), extending some distance into the lobe of the tail and supporting the ridge scales, but not giving attachment to any of the fin-rays. The lower lobe has a similar apparatus of hæmapophyses (Plate LXX. C, *h a*), considerably longer than the former. They afford attachment to a numerous group of interhæmal ossicles, having pointed bases and broad flattened extremities, to which the fin-rays are attached. The rays are from seventy to eighty in number. The inferior ones are the strongest, and they decrease in size as they succeed each other to the furthest extremity of the fin. The lower margin of the fin is destitute of fulcral scales, and is bounded by true fin-rays, elongating rapidly in succession until the maximum length of the lobe is attained. The bifurcations of the rays occur at very irregular intervals; they are more frequent in the

distal parts than in the vicinity of the base. The transverse joints are very frequent in all the rays. The upper lobe is invested, from the base to the extremity, with numerous rows of thick narrow imbricated scales, lozenge-shaped near the base, but elongating more and more until they become almost acicular at the distal termination of the fin. The pedicle of the tail is robust, in proportion to the length and spread of the organ it supports, which, both as to size and mechanism, is the most powerful instrument of progression yet met with amongst extinct fishes.

*Cranial Anatomy.*—The skull of the extinct Sturgeon (so far as one can judge from the confused and dislocated condition of its component parts in the specimens examined) corresponds with that of the recent Sturgeon in being composed of a semi-ossified cartilaginous box, protected by a series of bony plates. Of the bones composing the maxillary arch, the palatals (Plate LXIX. <sup>20</sup>) are most easily recognized. They are situated immediately in front of the epitympanic bones, and spread upwards, downwards, and backwards, occupying a large area, and having their broadest expanse directed forwards. They are thick and of compact structure, and having consequently resisted the effects of time more successfully than the slighter and more destructible parts, are of more frequent occurrence in the fossil specimens. The posterior process of the palatine bone is more prolonged than the corresponding part of the recent Sturgeon, and the lower anterior process to which the maxillary and premaxillary bones attach, is more expanded. The result of this character would be a more complete closure of the anterior roof of the mouth by the substitution of bone for cartilage than is the case in the existing Sturgeons. The upper anterior process is also broad for the attachment of the corresponding bone of the opposite side.

On comparing the fossil palatal bone with the recent one, the former so much resembles the latter *inverted*, that were it not for the conclusive evidence of several specimens having these bones in their proper position, the error might have been committed of describing the longer process as the anterior one, and *vice versâ*. That portion of the premaxillary bone (Plate LXIX. <sup>22</sup>) forming the trenchant margin of the upper jaw, resembles the homologous part of the recent Sturgeon, but the long posterior process which bends backwards and downwards in the latter, turns upwards in the former. The anterior plate is triangular, and is composed of hard bony material, having a rugged outward surface occasioned by the radiation of bony fibres from a central point of ossification. It is attached to the anterior lower process of the palatine bone, and connected with its fellow on the median line. The upward direction of the long process is a material deviation from the modern type; in the latter this process overlaps the articulation of the lower jaw, whereas in the fossil genus it rather simulates a nasal process. The distal extremity, instead of being flattened as in the Sturgeon, has a rounded termination as if for articulation with the nasal cartilages, or with the corresponding process of the opposite side.

There is no satisfactory evidence in any of the specimens examined of the character of the maxillary bone. A small bifurcate bone (Plate LXIX. <sup>21</sup>) is occasionally preserved

in a position which leads to the inference that it may be the posterior portion of this bone. It proceeds from underneath the premaxillary, and has an upward process overlapping the palatine bone, and a downward process extending in the direction of the articulation of the lower mandible\*. The lower jaw (Plate LXIX. <sup>32</sup>) is composed of a pair of single bones, narrow in front, and gradually expanding as they recede from the symphyseal suture. Their upper margins are edentulous. Their outer surface is corrugated, like that of the premaxillary bones, the rugæ being longitudinal. In a depression between two of the central rugæ, a series of minute apertures are discernible, for the passage of the vessels.

The maxillary and mandibular arches are suspended, as in the recent Sturgeon, from the tympanic pedicle. Of the bones and cartilages constituting this apparatus, the epitympanic bone (Plate LXIX. <sup>28</sup> *a*) is the part most easily identified, and most constantly preserved. It is seen sloping backwards and downwards from a point corresponding with the mastoid process of bony fishes. The articulating process and the upper third of the shaft are rounded; the lower extremity is expanded into a thin and broad plate. Compared with the epitympanic bone of a recent Sturgeon, it differs in being longer and thinner. The upper extremity is smaller and the lower broader, and more triangular in outline, and the entire bone constitutes a far larger portion of the arch. The succeeding elements, namely, the mesotympanic and hypotympanic, which are represented in the Sturgeon by two cartilages, are united to form one bony plate (Plate LXIX. <sup>28</sup> *d*), somewhat crescentic in form and having a tuberosity on the interior face, at a point corresponding with the junction of the two parts, for the attachment of the hyoidean arch. This compound bone is small and feeble compared with the great strength and expanse of the epitympanic. The upper extremity which meets the anterior angle of the spatulate termination of the epitympanic is thin and pointed, and ill-adapted, either in form or dimensions, for affording an articulation of sufficient strength for the support of the mandibular and maxillary organs. It probably represents merely the thick anterior column of cartilage, which in the recent Sturgeon is of great strength and solidity; the remainder of the attachment being completed by a plate of cartilage. The hypotympanic portion of the bone is also thin, but rather stronger than the upper half. It meets the condyloid extremity of the lower jaw at an open angle. This joint, as well as the connexion with the palatine bone, was probably completed by cartilages, as in the recent type.

The dislocated condition of the specimens renders it difficult to determine the constituent parts of the hyoid arch. In two instances, a single, broad umbonated bone (Plate LXVIII. fig. 2, <sup>42</sup>) is seen behind and below the symphysis of the lower jaw, which must be considered either as composed of the two basihyals united to form a keystone of the arch, or as the homologue of the great glossohyal or lingual bone found in the recent genera *Arapaima*, *Elops* and *Amia*, and in the extinct genus *Lophiostomus*. A bone (Plate LXVIII. fig. 2, <sup>40</sup>), which probably represents one of the

\* It is not improbable that this may prove to be the premaxillary, and that described as the premaxillary, the maxillary bone.

ceratohyals, occurs in several specimens in a position which leads to that conclusion. It has flattened extremities and a constricted shaft, resembling in outline two isosceles triangles united at the apices. The corresponding bone in the Sturgeon is shorter, broader, and thicker in all its dimensions. In one specimen a series of eight or nine plates (Plate LXIX. 44) is preserved, indicating the existence of the appendages of the hyoid arch, which are wanting in the recent Sturgeon. These homologues of the branchiostegous rays of bony fishes are flat, elongated bony laminae, of which the upper one is the longest. They are seen in their natural position, behind the hyoid bones and immediately below the opercular flap. They have the ganoid character of the corresponding parts in the fossil genus *Pachycormus*, but are fewer in number than in that and the allied genera. The only portions of the branchial arches I have been able to determine are the epibranchials (Plate LXVIII. fig. 2, *a, b, c, d*). These are four in number. The first or anterior bone is the longest. The upper extremity is broad and thin, the shaft and lower extremity slender and cylindrical. The two succeeding bones are less expanded above and are rather shorter. The last of the series differs from the others in having its broader extremity directed downwards. It is in fact very similar in form to the ceratohyal bone, but differs in having the upper extremity and the shaft rather more cylindrical. The number corresponds with that of the homologous parts of bony fishes, if we limit the term branchial arch to the gill supporting bones, to the exclusion of the pharyngeal arch. The proportions of the epihyals in the fossil correspond with those of the same parts in most of the bony fishes, the first being the longest, and the fourth the shortest, with a broad inferior articulation.

The sphenoid bone (Plate LXVIII. fig. 1, *9*), constituting the base or platform of the cranial cavity, is more completely ossified in the extinct than in the recent Sturgeon; hence its preservation in the fossil state. The anterior or presphenoid portion of the bone (Plate LXVIII. fig. 1, *9*) is extended forwards beyond the palatal bones, and the basisphenoid (Plate LXVIII. fig. 1, *5*) projected backwards to the point of junction of the trunk with the head. The posterior termination of the bone was deeply notched, and so thin, that the non-existence of a distinct basioccipital bone is made evident from the absence of any articulating surface for its attachment. The alisphenoid processes (Plate LXVIII. fig. 1, *9*) are given off at a point considerably in advance of the position they occupy in the generality of bony fishes; they correspond very nearly in this respect with the homologous parts of the Sturgeon. They are situate, in the fossil,  $3\frac{1}{2}$  inches from the posterior, and 2 inches from the anterior extremities of the bone. This extension of the bone backwards in both the recent and fossil Sturgeon, so remarkable in comparison with the relative dimensions of the elements of the sphenoid bone in the *Teleostei*, is considered by Dr. RUDOLPH WAGNER to be effected by the calcification of the fibrous sheath of the basioccipital and postsphenoidal regions of the chorda dorsalis; Professor OWEN, however, considers that its extension upon the neck, the absence of the articular concavity, and the persistence of the cartilaginous basis of the skull, are opposed to this view of its homological relations.

It has already been stated, in the description of the organs of locomotion, that in the

caudal region the processes both above and below the vertebral column were bony and persistent. In the anterior parts of the trunk, the former, or neurapophyses, are present, but the hæmapophyses are in no case preserved; the latter, together with the vertebral centra, were composed of perishable material unable to resist the process of decomposition, which the harder parts successfully withstood. Professor OWEN describes the neural arch of the vertebra in the Sturgeon as composed of "two superimposed pieces on each side, the basal portion bounding the neural canal, the apical portion the parallel canal filled by fibrous elastic ligament and adipose tissue; above this is the single cartilaginous neural spine\*." The corresponding parts in the fossil connected with the anterior portion of the column are preserved in one specimen. The neurapophyses (Plate LXIX. *n a*) are expanded at each extremity, and slightly constricted in the middle region. They appear to be composed of two elements, corresponding to the basal and apical cartilages in the Sturgeon; but whether the latter embraced a second canal parallel to and above the spinal chord, I am unable to determine. Probably the substitution of bone for cartilage in the extinct genus may have rendered the support of the fibro-cartilaginous substance contained in this canal superfluous. The neural spines (Plate LXIX. *n s*) are higher than those of the Sturgeon. The highest, although not perfect, measures three-quarters of an inch. These, together with the apophyses which support them, slope backwards at a considerable inclination; but by a curve forwards at a little distance from the articulation, the former show a tendency to assume a perpendicular position. The breadth and proximity of the neural arches must have given great support and protection to the weaker parts of the spinal column.

*Dermal Bones.*—The roof of the cranial cavity of the extinct Sturgeon was composed, as in the recent fish, of indurated plates united to each other by close sutures. Before entering upon the description of these several parts, it is advisable to premise a few observations on the corresponding parts of the existing Sturgeon. Many attempts have been made by comparative anatomists to recognize in these cranial plates the homologues of the true epicranial bones of the bony fishes, but no conclusions have been as yet received as satisfactory. The discrepancy and irregularity observable in the size, form, and number of the head-plates, not only in the different species, but even in individuals of the same species, have been considered good and sufficient grounds for demurring to the several theories advanced as to their special and general homologies. Having had occasion to examine a considerable number of recent crania while investigating the affinities of the fossil Sturgeon, I have observed a great want of uniformity between the outer and inner demarcations of the principal cranial plates, and that, although the former may vary in number and relative proportions, the latter are constant and symmetrical. This nonconformity is frequently so marked, that a bone, single and well-defined on the inner table of the skull, may be invested with two or more scutes on the dermal surface. The suprascapular bone, for instance, usually carries two scales externally, in consequence of which deception the upper one has been con-

\* Hunterian Lectures, 8vo, 1846, vol. ii, p. 53.

sidered the representative of the parietal bone, a misnomer which must of necessity invalidate the implied relations of all the surrounding parts. The knowledge of the true demarcation of this bone leads to the exposure of another error which has embarrassed the solution of this question, namely, the idea that the large posterior median plate represents the supraoccipital bone, whereas it must be considered as belonging to the series of dorsal plates, and may be designated as the nuchal scale. In front of this a smaller median plate is situated, which may with more probability be referred to the supraoccipital region. This is flanked on either side by a small lateral plate in the position of the paroccipitals, to which and the exoccipital the upper extremities of the suprascapular bones are articulated. Beneath and behind the paroccipital two plates are attached, having broad alæ descending into the cranial cavity. These may be considered the exoccipitals, or lateral elements of the neural arch of the first occipital vertebra. The upper extremity of the suprascapular and the exoccipital bone are covered externally by a single scale, concealing the junction between the two. The arch of the second cranial segment is composed of two pairs of large elongated plates. The outer pair are characterized by well-developed processes, extending downwards and inwards to meet the corresponding extremities of the alisphenoids, a character which affords strong reasons for considering them the true homologues of the mastoid bones. They extend backwards as far as the par- and ex-occipitals, and are united in front with the frontals and postfrontals. The centre pair of plates are the parietals. They articulate with the paroccipitals and the supraoccipital. The latter sends out a long median process between the parietals, in advance of which a small midfrontal plate occurs, occupying the position of the fonticelle, observable in the young Sturgeon, and sometimes present in the bony fishes, both recent and fossil. The parietals are connected laterally with the mastoids, and anteriorly with the inner posterior margins of the frontals. The third segment of the cranium is likewise composed of two pairs of plates, representing the frontals and postfrontals. The former are wedged posteriorly into the angles between the extremities of the mastoid and parietal plates, and extend forwards beyond the nasal aperture; they are flanked by the outer pair of bones, the postfrontals. These are united behind to the mastoids by strong squamose overlaps, from which points the tympano-mandibular arch is suspended.

The truth or fallacy of the homologies I have attempted to trace in the indurated portions of the cranial cartilages, must depend upon more extended investigations of the softer tissues entering into the cranial æconomy, both in the embryonic and adult conditions; in the meantime, by adopting (if only provisionally) the analogies now proposed, one object I have in view will be obtained, namely, the use of intelligible terms for comparison between the recent and fossil Sturgeons. The description given by Professor OWEN, in his 'Lectures on Comparative Anatomy,' of the cartilaginous elements of the cranial bones of the Sturgeon, tends to verify the positions I have assigned to the indurated parts in the epicranial table; the difficulties which have hitherto embarrassed the subject I have attempted to overcome, by showing that these parts are composed of an

outer and an inner layer, and that although the former may, through the irregularity of its configurations, lead to erroneous suppositions as to the coincidence of its several compartments with the true cranial bones, the latter is sufficiently constant to lead to reasonable conclusions as to the homologies of its associated members.

The only portions of the cranial covering of the fossil Sturgeon as yet discovered are the parietals, the mastoids, the frontals, and the prefrontals. A small plate observable in one specimen may perhaps represent the paroccipital. None of the single median plates are indicated in any of the specimens. As a general character, all the head-bones are relatively much shorter and broader than those of the recent Sturgeon. This feature is in harmony with the short and bulky form of the trunk. The parietal plates (Plate LXIX. 7) are oblong, measuring about an inch and a half in length by three-quarters of an inch in breadth. They articulate with each other on the median line, without the intervention of the prolonged process of a supraoccipital plate. Each has a slight central umbo, from whence the fibres radiate outwards to the periphery. The mastoid plates (Plate LXIX. 8) are of larger dimensions, measuring an inch and three-quarters in length by an inch and eight-tenths in breadth. In disjointed specimens they are easily distinguished from the parietals by the position of the umbo from which the bony fibres radiate, this being situated on the outer margin of the plate. They articulate by their inner margins with the parietals. The frontals (Plates LXVIII. fig. 1, and LXIX. 11) are remarkable, in comparison with their recent homologues, for great width and contraction of the antero-posterior diameter. They measure an inch and a half in length by one inch in breadth. The corresponding dimensions of these plates in the recent specimen, from which former comparative measures have been taken, are two inches by six-tenths of an inch. The frontals articulate posteriorly with the parietals and mastoids, and, on the median line, with each other, without the interposition of a midfrontal plate or fonticelle. The centre of each plate is slightly elevated. A portion of a postfrontal plate (Plate LXIX. 12) is visible in one specimen, articulating with the frontal and mastoid. All these plates are united and interlocked by means of coarse sutures, and not by squamose overlaps, as in the recent Sturgeon. On the outer surface they are for the most part smooth, and seem to have been covered by a soft integument. A few superficial granules are scattered irregularly over some of the specimens (which may perhaps be a specific character), but there is no evidence of the deep pits and coarse radiating ornament so characteristic of the dermal scales of the Sturgeon. The same absence of surface ornament obtains with reference to the opercular apparatus. The operculum (Plates LXVII. and LXIX. 35) is a broad and flat plate, almost circular, and exceedingly thin. It has no articulating facet on the upper margin, and was probably suspended in the tegumentary tissues, deriving a certain amount of additional support from the broad posterior limb of the epitympanic bone. The outer surface is smooth and very compact. The inner surface is characterized by the occurrence of numerous minute punctures passing obliquely into the substance of the plate. The posterior outline is semicircular, adapting itself to the anterior curve of the thoracic cincture. The lower



edge is straight, and gives attachment to a small subopercular plate (Plates LXVII. and LXIX. <sup>36</sup>), having a still smaller interoperculum (Plates LXVII. and LXIX. <sup>37</sup>) fitted to its anterior margin. These are succeeded below by the branchiostegous rays described in a former part of this memoir. This arrangement of the opercular apparatus corresponds with that of some of the extinct fossil fishes. The preoperculum is wanting. The external characters of the cranial envelope tend to the conclusion that the dermal crust was very feebly developed in this region, and lead to the further inference that a proportionate deficiency would be found in other parts of the tegumentary covering. This was probably the case, for with the exception of the scales investing the caudal fin, no trace has been discovered of the dermal plates, so characteristic of the recent Sturgeon. The negative evidence of the non-existence of this peculiar feature is strengthened by the fact, that of all the component tissues these dermal plates are the most indestructible, and would therefore have resisted decomposition more effectually than other more tender parts, which are nevertheless found in the fossil state. The broad nuchal scale, for instance, so prominent in the recent Sturgeon, would have left some trace of its existence in specimens, where not only the surrounding bones, but even the semicartilaginous remains of the subjacent vertebral neural arches, are distinctly preserved.

Another feature bearing upon this question is seen in the natatory organs. In the recent Sturgeon, the dorsal, anal, and caudal fins are each provided with a short anterior spine springing from a dermal plate, whereas in the fossil species no such spine-bearing scales occur, the first fin-rays being supported by interapophysial osselets, as in other bony fishes. In one specimen examined by me, a portion of the skin is preserved. Viewed under the microscope, all structure characteristic of dermal tissue is obliterated, and the substance resembles a thin layer of carbonaceous material, perfectly homogeneous, and showing no trace of the bony spiculæ, which to a greater or less extent beset the smooth portions of the skin in the recent Sturgeon. I am therefore inclined to think that the fossil Sturgeon was smooth and scaleless, like the *Spatulariæ* of the North American rivers, although in other details of organization it had greater affinity to the more typical Sturgeons. Of these, the *Scaphyrhynchi* have the head-bones almost as smooth as those of the *Polyodon*, but the development of the dermal scales on the trunk is excessive, the caudal region being wholly encased with defensive armour. In some species we see the dermal layer thick and rugged on the head, and yet feebly developed in the trunk; while in others the deposition of bony material is coextensive on both the head and body. With regard to form, some are long and slender, others are more massive; some have elongated snouts, others have the rostrum more abrupt.

Of all the species I have examined, *Acipenser Guldenstädti* has the nearest resemblance to the fossil genus. The short snout, the proportions of the cranial plates, and the depth of the anterior part of the body, are to a certain extent approaches to the condition of these parts in the extinct form, and they are combined with the minimum amount of calcification of the integument; at the same time these are features of minor

importance to the more remarkable and distinctive characters which stamp the generic discrepancy of *Chondrosteus* from all existing forms of fish\*.

*Specific characters.*

The collection of Fossil Fishes in the British Museum contains two specimens of *Chondrosteus*, showing some of the head-bones and a pectoral fin of individuals of gigantic proportions. Mr. HARRISON, of Charmouth, has kindly forwarded for inspection a tail of proportionate size, and which is supposed to have belonged to the same individual as one of the Museum specimens. Although size alone is no criterion of specific difference, it is nevertheless of some importance in this instance, where out of a very large number of specimens found in one locality, some are so greatly disproportioned as to be easily eliminated, while none afford any evidence of gradation from large to small. It is not, however, necessary to rely upon size alone in this case, since it is associated with other peculiarities constituting specific characters. The only portions of the head recognizable in the specimen in the British Museum are the parietal and mastoid bones. The surface of these is rough and granular, showing a considerable amount of dermal consolidation. The outer posterior angles of the mastoid bones are extended backwards, and afford articular surfaces for the attachment of the upper extremities of the suprascapulars. One of the latter bones is preserved, and measures 6 inches in length. The tail, from the collection of Mr. HARRISON, measures 18 inches in length. The lower lobe is imperfect, but the total expanse of the organ cannot have been less than 20 inches. The length of the entire fish must probably have been above 5 feet. The most remarkable character of the caudal fin is the excessive development of the scales bordering the upper margin. The size and solidity of these scales is such that they more resemble the broad teeth of an *Acrodus* than any dermal development with which I am acquainted. In consequence of this peculiarity, I have named this species *Chondrosteus pachyurus*. The numerous specimens derived from smaller individuals present indications of two species, one having the bones of the head thin and smooth, the other being characterized by stronger cranial plates, having a granulated exterior. The anal fins of the latter are more massive, and have the transverse articulations at shorter intervals (Plate LXX. A). I propose to retain the Agassizian name *Chondrosteus acipenseroides* for the former, and to designate the latter as *Chondrosteus crassior*.

*General remarks.*—The Sturgeons were considered by CUVIER, in his classification of fishes, to belong to the great subdivision designated, in consequence of the cartilaginous condition of the endoskeleton, *Pisces cartilaginei*; Professor AGASSIZ, however, in his great and successful effort to incorporate in one general system both the recent and extinct fishes, included them in his newly constituted family termed *Ganoidei*, from the peculiar characters of the exoskeleton. The propriety of the latter classification has been fully substantiated by Professor JOHN MÜLLER, who, after a most careful

\* The gigantic fossil fish of the Whitby Lias, named by AGASSIZ *Gyrosteus mirabilis*, belongs to the Sturionidæ, and is nearly allied to *Chondrosteus*.

and elaborate examination and comparison of those recent fishes most calculated to throw light upon the subject, has concluded—1st, that the Ganoidei form a well-defined order between the true osseous fishes and the Selaceans; and 2ndly, that AGASSIZ'S view of the position of the Sturgeons amongst the Ganoidei is correct. Professor OWEN considers the Sturgeon to be “one of the transitional steps from the cartilaginous to the osseous fishes,” and adds the weight of his testimony to the soundness of Professor AGASSIZ'S views in arranging the Sturionidæ under the ganoid order of fishes. The conclusions arrived at by these distinguished authorities resulted from the examination and comparison of the recent Sturgeons and the recent and extinct Ganoids; no evidence having been then obtained of the occurrence of the former family in the fossil state. The discovery, therefore, of a representative of the Sturionidæ in the earliest oolitic deposits, a period in which the typical ganoid fishes attained their maximum of numerical development, has a material bearing upon this subject, inasmuch as it supplies the only term of comparison wanting in the inquiry. The opportunities which I have had of examining all the specimens hitherto brought to light, have enabled me to ascertain most of the significant features of the liasic Sturgeon, the descriptions of which I have embodied in the foregoing memoir. The results may be briefly summed up as follows:—

1st. That in all essential particulars, more especially in the arrangement of the cranial plates and the oral apparatus, in the persistence of the chorda dorsalis and partial ossification of its peripheral elements, the fossil Sturgeon closely resembled the recent form.

2nd. That in the structure of the opercular and hyoid regions, and in the greater extent to which the ossification of the endoskeleton had proceeded, it approached the condition of these organs in the ganoid fishes, and constituted a transitional form between these and the recent Sturgeon.

3rd. That its bulky form and smooth integuments, contrasting so strongly with the tapering body and dermal armour of the Sturgeon, afford a striking instance of the universal law of special modification of organization for peculiar conditions of animal existence.

The Sturgeons of our own time, inhabiting the bottoms of the estuaries of mighty rivers, subject to frequent paroxysmal inundations, require not only an external form of least resistance, combined with powerful propulsory organs, to withstand the torrents to which they must necessarily be exposed in procuring their daily subsistence, but also a defensive armour sufficient to fortify their bodies against injury from stones and other detrital matters hurried down by the force of the streams. The liasic Sturgeons enjoyed a more tranquil existence. The evidence of the associated molluscan and radiate forms, proves the marine character of the waters they inhabited; the thinly laminated beds of shale and limestone from which their remains are exhumed, testify to the tranquil condition of the sea in which they lived; their smooth skin, harmonizing in tint with the muddy bottom on which they reclined, served to conceal them from the predatory Saurians and larger fishes with which they coexisted; they required neither defensive armour nor locomotive energy for self-preservation in the fulfilment of those special

functions assigned to them in this ancient ocean, although probably of the same nature as those performed now by the surviving representatives of the family.

## EXPLANATION OF THE PLATES.

## PLATE LXVII.

*Chondrosteus acipenseroides*, AGASSIZ:—reduced one-fourth.

## PLATE LXVIII.

Fig. 1. Head and pectoral fins of *Chondrosteus crassior*, EGERTON:—reduced one-third.

Fig. 2. Outline of the head of Plate LXVII.

## PLATE LXIX.

Anterior portion of *Chondrosteus acipenseroides*, AGASSIZ:—reduced one-fourth.

## PLATE LXX.

Anal and caudal fin of *Chondrosteus crassior*, EGERTON:—natural size.

## NOTATION OF PARTS.

P. Pectoral fins.

D. Dorsal fin.

C. Caudal fin.

5. Basisphenoid.

6. Alisphenoid.

7. Parietal.

8. Mastoid.

9. Presphenoid.

11. Frontal.

12. Postfrontal.

20. Palatine.

21. Maxillary.

22. Premaxillary.

28 *a.* Epitympanic.

28 *d.* Hypotympanic.

32. Dentary.

35. Opercular.

V. Ventral fins.

A. Anal fin.

36. Subopercular.

37. Interopercular.

40. Ceratohyal.

42. Glossohyal.

44. Branchiostegal.

50. Suprascapular.

51, 52. Scapulocoracoid.

57. Metacarpal.

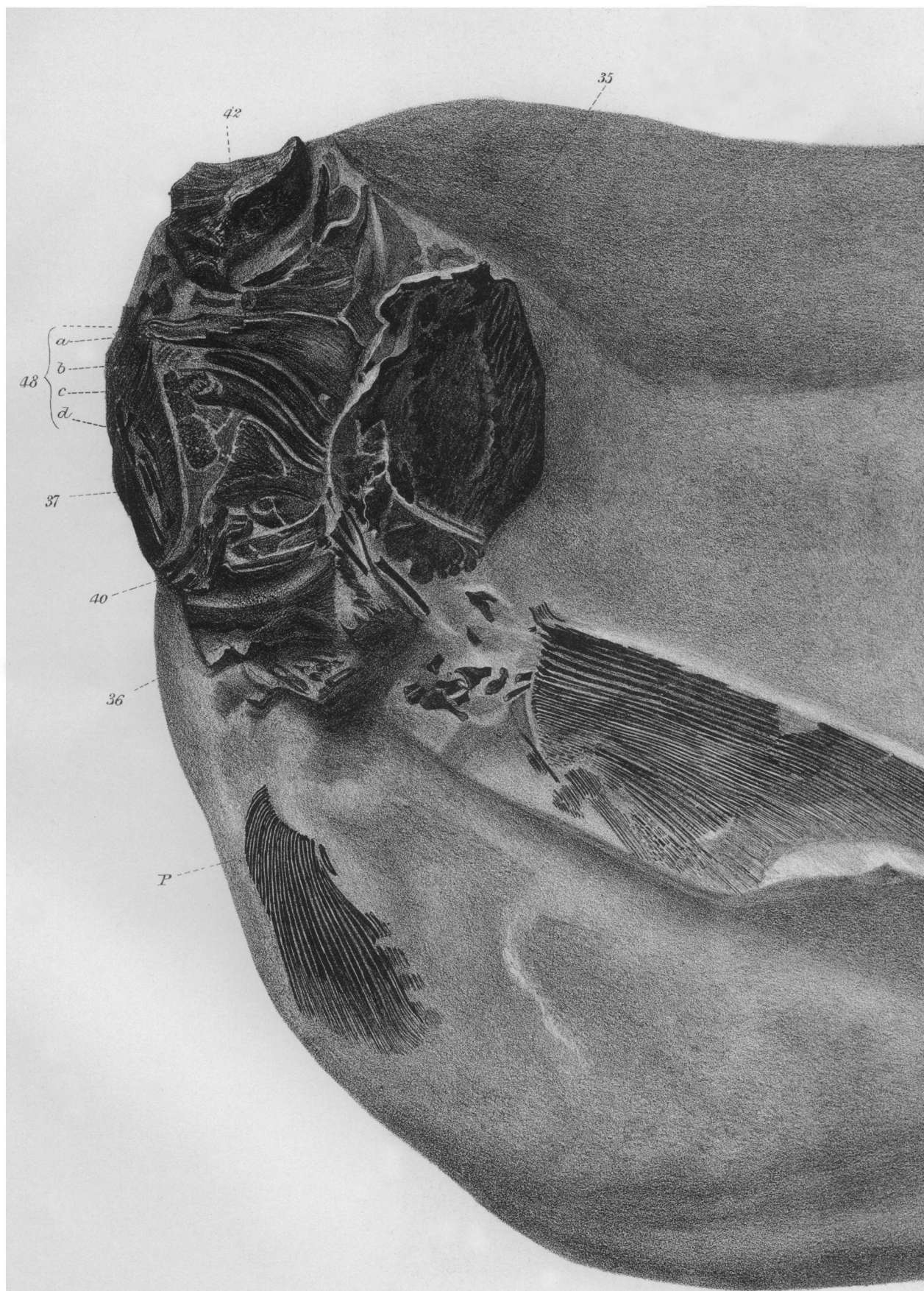
69. Metatarsal.

*n. a.* Neurapophysis.

*n. s.* Neural spine.

*i. n.* Interneural spine.

*i. h.* Interhæmal spine.







*D*



*A*







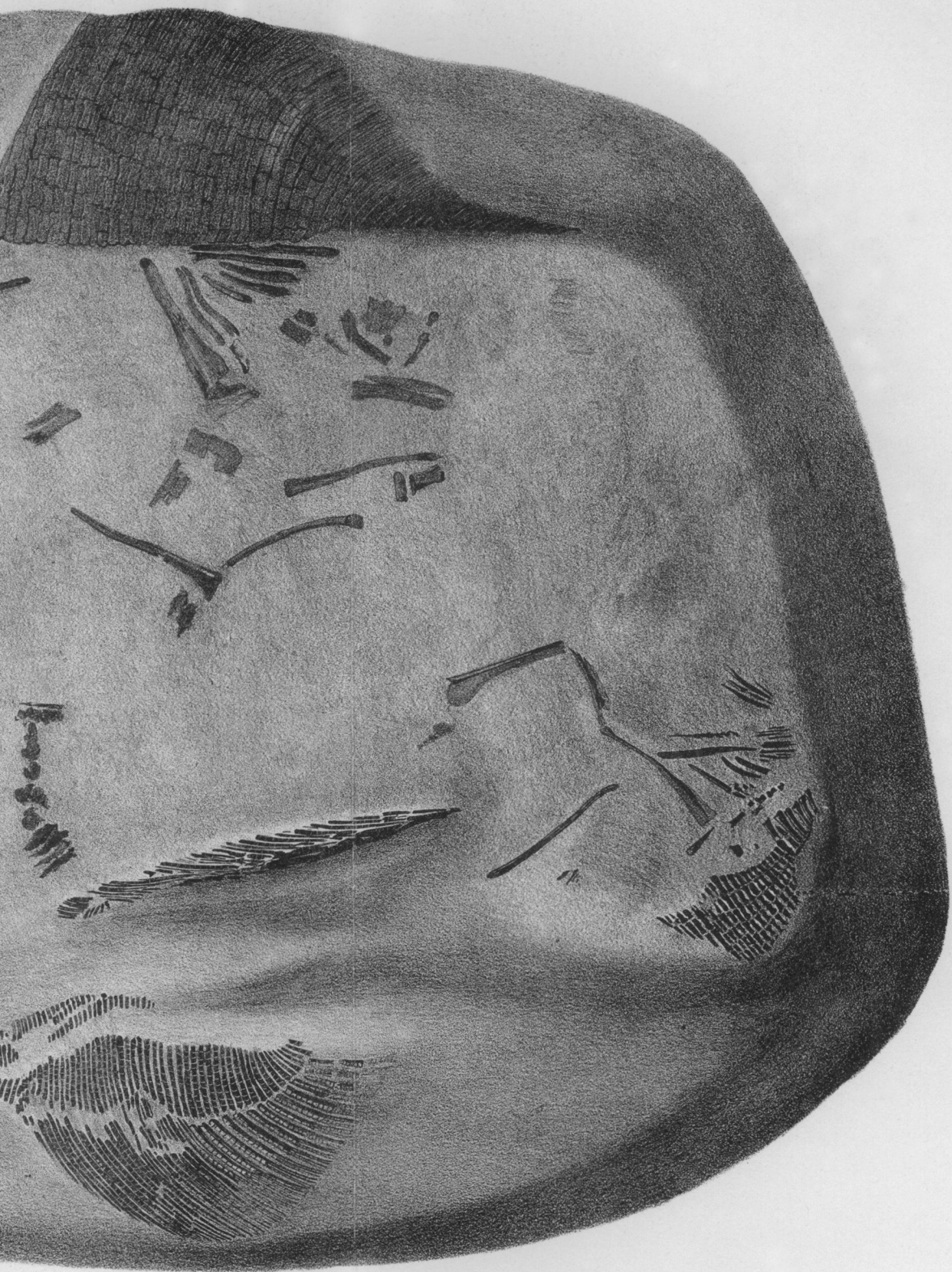


*Reduced  $\frac{1}{4}$ "*

V

CHONDROSTEUS ACIPENSEROIDES.

D



A

V



Fig. 1.

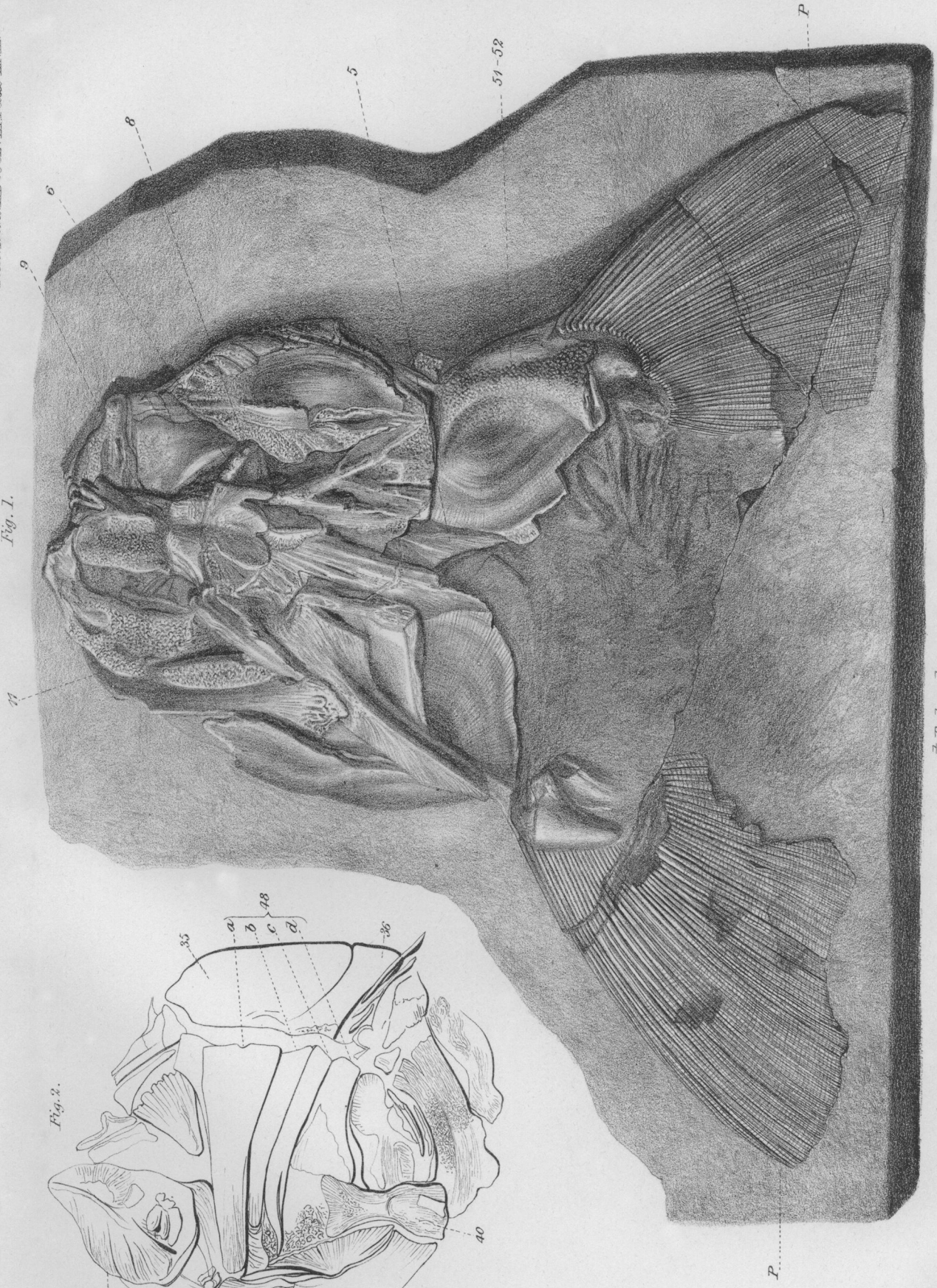
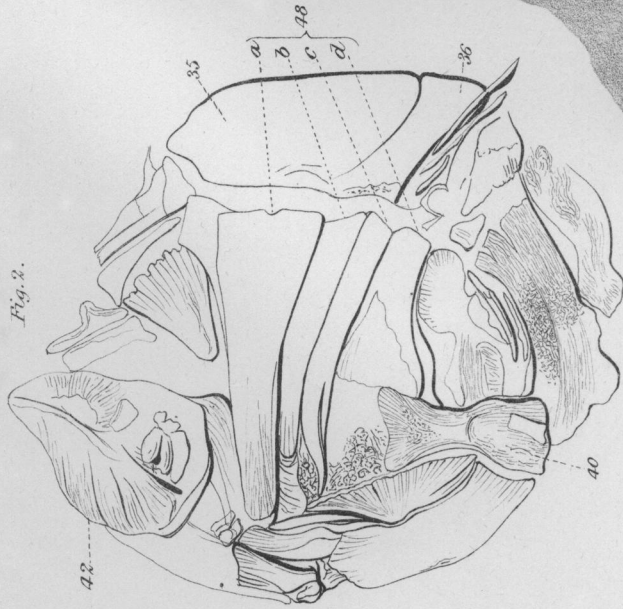


Fig. 2.



J. Dinkel, Lith.

$\frac{2}{3}$  Reduced.

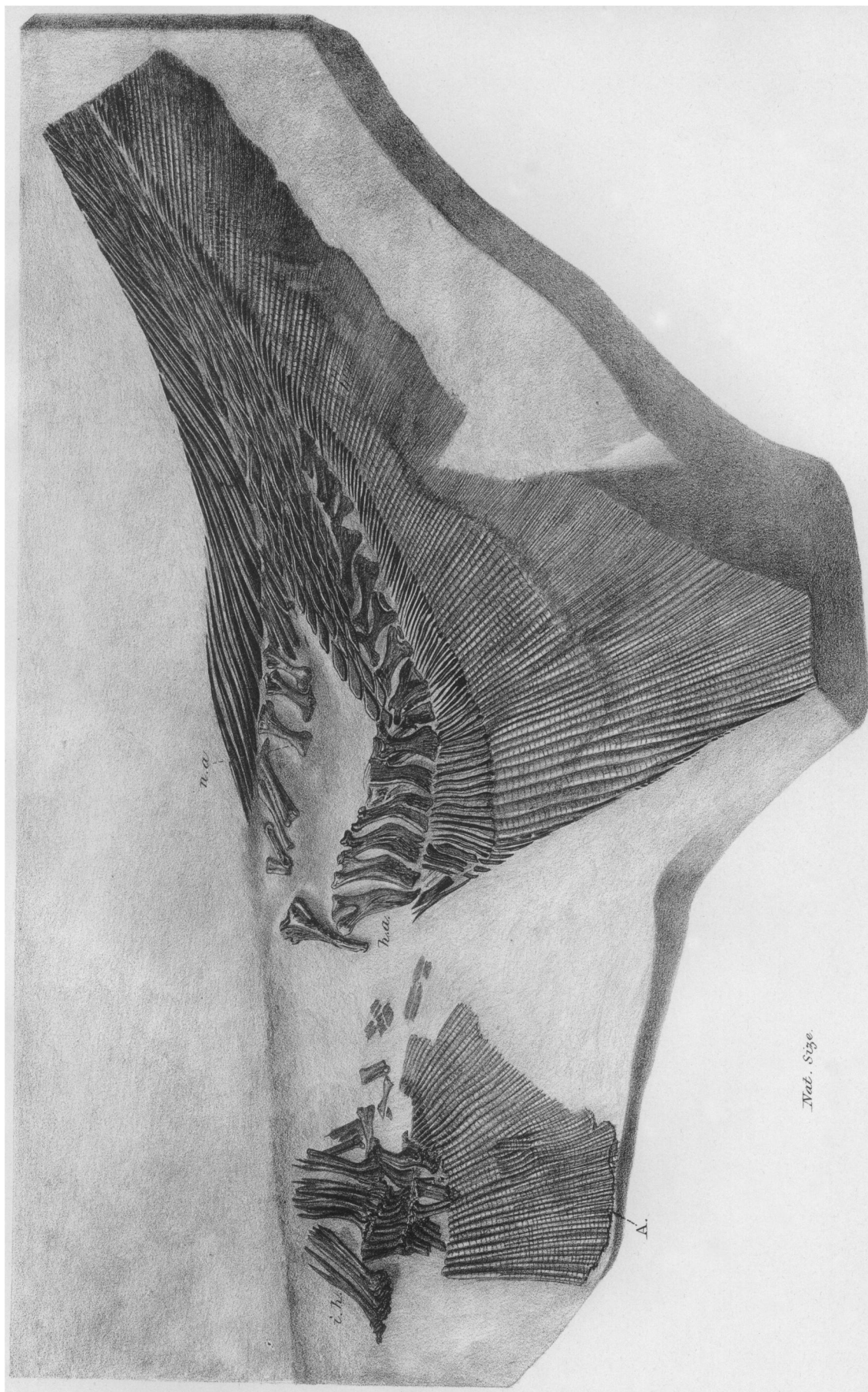
CHONDROSTEUS CRASSIOR. EGERTON.

Printed by J. Baskin.



CHONDROSTEUS ACIPENSEROIDES AGASS.





*Nat. Size.*

*J. Dunkel. Lith.*

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